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EFFECTS OF FEEDING, FEEDING HISTORY, AND FOOD DEPRIVATION ON RESPIRATION AND EXCRETION RATES OF THE BATHYPELAGIC MYSID *GNATHOPHAUSIA INGENS*

PAGE HILLER-ADAMS AND JAMES J. CHILDRESS

Marine Science Institute, Department of Biological Sciences, University of California, Santa Barbara, Santa Barbara, California 93106

Abstract

Groups of the large bathypelagic mysid *Gnathophausia ingens* were fed at different frequencies for at least three months in the laboratory, then starved for five weeks or alternately fed and starved over shorter periods of time. Oxygen consumption and ammonia excretion rates were determined before and after feeding and during starvation. Prolonged differences in the amount of food eaten prior to starvation affected the animals' initial responses to starvation. In the first 3 weeks, animals which had been more frequently fed maintained higher respiration and ammonia excretion rates relative to rates after this time. Animals fed less frequently maintained stable rates throughout the 5 week period of starvation. After a maximum of 3 weeks, starved individuals relied largely on nonnitrogenous energy stores, presumably lipids, regardless of feeding frequency prior to starvation. The high lipid content of *G. ingens* and the low metabolic rate of starved individuals are advantageous for life in the energy-poor deep-sea.

We have observed transient postfeeding increases in respiration and excretion rates. Excretion rate (E, in micromoles NH_3/h) increased with amount eaten (F, in mg ash-free dry weight of food) ($E = 0.038F$). Respiration rate (R, in micromoles O_2/h) increased with excretion rate ($R = 1.40 + 1.03E$). Measurements of respiration and excretion rates using postdigestive individuals of *G. ingens* therefore underestimate average field rates by an amount proportional to food intake. The energetic effects of feeding on the metabolism of *G. ingens* are not negligible. We estimate that about 29% of the energy in the laboratory ration ingested by *G. ingens* is expended in the postfeeding increase in respiration.

Introduction

The dramatic decrease in biomass of the world's oceans with increasing depth, and the generally patchy distribution of animals living in the water column, suggest that food scarcity is one of the most physiologically important characteristics of the deep sea. Food scarcity may in part be responsible for characteristics of the chemical composition (Childress and Nygaard, 1973, 1974), metabolic rates (Childress, 1971a, 1975; Smith and Hessler, 1974; Torres *et al.*, 1979), and life histories (Childress and Price, 1978; Childress *et al.*, 1980) of deep-sea animals. Information on the metabolic responses of deep-sea animals to feeding and to food deprivation should therefore add to our knowledge of the physiological and energetic adaptations of deep-sea animals to their environment. The responses may also be compared to those of shallow water animals which live in an environment which is physically more variable. This paper presents the results of an investigation of the effects of feeding, food

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deprivation, and feeding history on the respiration and excretion rates of the large bathypelagic mysid *Gnathophausia ingens* Dohrn. We have investigated the effects of feeding frequency prior to prolonged periods of starvation on respiration and excretion rates during starvation and on the substrates metabolized during starvation. We have also quantified the relationships between food intake and transient postfeeding increases in respiration and excretion by this species, and estimated the energetic importance to *G. ingens* of these increases.

G. ingens is well-suited to such a study since individuals can be obtained in relatively large numbers off the coast of southern California, and may be maintained for relatively long periods in the laboratory (up to 2.5 years: Childress and Price, 1978). The life history of *G. ingens* is well known (Childress and Price, 1978). Females brood their young at depths between 900 and 1400 m. Newly released young ascend to depths of about 175–300 m. On reaching the fifth instar (carapace length between 14.2 and 17.7 mm: Childress and Price, 1978) they descend to depths of 650–750 m, dispersing at night to depths of 400–900 m. After the fifth instar, individuals live permanently beneath the photic zone.

Materials and Methods

Animal capture and maintenance

Individuals of *Gnathophausia ingens* were captured in San Clemente and San Nicholas Basins off the coast of southern California during January and April 1979, using an opening and closing 3.3 m × 3.3 m Tucker trawl equipped with a thermally protecting cod-end (Childress *et al.*, 1978). We removed live individuals from the cod-end as soon as it arrived on deck, wrapped them loosely in nylon mesh, placed them in 1 gallon jars filled with sea water, and maintained them at approximately 5°C. On our return to the laboratory, each animal was unwrapped and put in a container of about 700 ml of chilled sea water, and placed in the laboratory cold room (5.5°C). The room was dark except for occasional short (several minutes) periods during the day when laboratory personnel entered. After two weeks in captivity, each animal was assigned a number and all the animals were alternately fed salmon muscle and ridgeback shrimp (*Sicyonia incertus*) tails according to the feeding regimes described below. Maintenance water was changed once every 2–3 weeks, and after each feeding.

All animals were maintained at atmospheric pressure. We believe that this does not bias the results since this species can live and grow in the laboratory for periods of up to 2.5 years at atmospheric pressure (Childress and Price, 1978). Further, research in this laboratory has shown that the respiration rates and activity of this and other midwater species are relatively unaffected by a pressure of 1 atm (Meek and Childress, 1973; Mickel and Childress, 1982). Our studies have also shown that *G. ingens* swim continuously at a rather fixed rate which does not decline in captivity (Quetin *et al.*, 1978; Quetin and Childress, 1980; Mickel and Childress, 1982). Our experience with this mysid therefore leads us to believe that our results are reasonably representative of the field situation.

Feeding

Individuals were fed either 6×/mo for 3.5 months ("6×/mo, 1st series"), 6×/mo for 5 months ("6×/mo, 2nd series"), 1×/mo for 3–4 months ("1×/mo"), or 6×/mo for 2 months followed by 3 months of feeding 2×/mo ("2×/mo"). Individuals were not offered food for two weeks after they had molted since they generally do

not accept food prior to this time. Feedings within each group were evenly spaced over time. Experiments in which respiration and excretion rates were determined began at the end of these feeding periods. *G. ingens* were fed shrimp during the experiments, except for two 1×/mo individuals which were fed salmon at the start of the experiment using 1×/mo animals. Only shrimp meals are considered in the analysis of postfeeding increases in respiration and excretion since all but two of the metabolic measurements were made after the animals had fed on shrimp.

To feed the animals, and to determine the amount eaten by each individual, a small preweighed piece of food was held near each animal until it grasped the piece with its pereiopods. Four to six hours later the remaining food was removed with forceps and with a perforated spoon which facilitated the removal of smaller pieces of food. All visible pieces of food were removed, and the water in each animal's container was replaced with fresh, chilled (5.5°C) sea water. The food which had been removed was placed in tared pans, dried to constant weight at 60°C and weighed (dry weight), then ashed to constant weight at 500°C and weighed again (ash weight). The difference between the dry weight and ash weight constituted the ash-free dry weight (AFDW) of the uneaten food. For each feeding, two preweighed pieces of food were placed in sea water without an animal for the duration of the feeding period and were similarly dried and ashed. These pieces served as controls for the loss of material from the food due to immersion. The AFDW available to the animals was estimated by multiplying the fresh weight of each piece fed to an animal by a conversion factor which was the average ratio of AFDW/fresh weight determined from the two control pieces. The ash-free dry weight of the food eaten by each individual could then be calculated as the difference between the "available" AFDW and final AFDW of its food.

We chose AFDW for quantification of food eaten because it is a measure of total organic matter and as such is a better estimator of food value than wet or dry weight, each of which include substantial amounts of inorganic material. Use of AFDW also avoids the complication of variable amounts of salt water on the surface of the left-over food. The method which we have used is a way to approximate the actual ingestion since some additional material may be leaked from the food during external chewing. The error from this source is probably minor since these animals typically ingest small pieces of food immediately after removing them from the main chunk.

The salmon and shrimp meals were the only significant sources of food for *G. ingens* since the species is not suited for filtering fine particles from the water (setae on the pereiopods are sparse), and since several studies have failed to detect significant uptake of dissolved amino acids by aquatic crustaceans (Stephens and Schinske, 1961; Stephens, 1972; Ferguson, 1982).

Protocol for respiration and excretion measurements

In a typical experiment, animals were removed from their open maintenance containers and placed in individual one-liter flasks containing sea water (5.5°C) to which 50 mg/l each of streptomycin and neomycin had been added. The sea water had been filtered either through a 0.45 micron membrane filter or through glass wool. The flasks, including two control flasks which contained only sea water and antibiotics, were closed with rubber stoppers. Care was taken to exclude all air bubbles. At the end of the experiment water samples were removed for oxygen and ammonia analyses and the animals were replaced in their maintenance containers. All experiments were conducted in the dark at 5.5°C.

Each experiment lasted from 8.5 to 10 hours. The duration was adjusted to

obtain measurable decreases in oxygen contents of the flasks without allowing the oxygen content to decrease below the level at which respiration rates become dependent on the partial pressure of oxygen (Childress, 1971b; Mickel and Childress, 1978).

Oxygen

Oxygen was analyzed using standard Winkler techniques (Strickland and Parsons, 1972). Flasks were unstoppered at the end of each experiment. A water sample for analysis of oxygen content was carefully siphoned from each newly opened one-liter flask into a 125 ml glass-stoppered flask, and Winkler reagents were added. Sample concentrations of oxygen were corrected for changes in the oxygen content of the control flasks. These changes were always less than 3% of the starting concentrations, which varied between 497 and 692 micromoles O_2/l. Oxygen consumption rates determined from duplicate titrations of single samples differed by an average of less than 2%.

Ammonia

The ammonia content of a 50 ml subsample from each one-liter flask was determined using an ammonia electrode (Orion Research, Inc., Cambridge, MA). Electrode potentials were converted to ammonia concentrations using an average of two standard calibration curves, one made immediately before and one immediately after sample analysis. To make each curve, known amounts of a standard ammonium chloride solution were added successively to 50 ml of sea water made basic (pH about 11) with sodium hydroxide. The sea water was continously mixed with a magnetic stirrer at low speed. After each addition, the electrode was allowed to stabilize before the electrode potential was recorded. The two curves for an experiment generally differed by less than 0.5 micromole/l for a given electrode potential in the sample concentration range. Consecutive measurements were repeatable to ±4%. Electrode drift was minimized by placing the electrode in sea water adjusted to pH 11 for 30 minutes prior to use. Concentrations of ammonia in the control flasks did not change detectably during any of the experiments.

Analysis of results

In comparing the physiological responses to food deprivation by animals on different feeding regimes, we considered only data for those individuals which survived the initial feeding period and the experimental period in which respiration and excretion rates were determined, and did not molt during the experimental period. There were four such 6×/mo (1st series) individuals (6.5–18.6 g), five 1×/mo individuals (5.5–11.8 g), four 6×/mo (2nd series) individuals (5.2–9.2 g), and two 2×/mo individuals (5.2 and 9.4 g) of an initial 9, 5, 6, and 4 individuals, respectively. Six of the original 24 animals (25%) died during the initial feeding period or during the experiment, and 3 (13%) molted and were not considered.

It is important to note that in each experiment in which individuals were starved we have compared and contrasted the trends in, rather than the levels of, respiration and excretion since the number of individuals available was small. Consistent differences in individual rates which in a small sample might unduly affect comparisons of means between groups, will not affect comparisons of individuals followed over a long period of time.

For analysis of short-term responses to feeding (responses occurring within a few days after feeding), we considered data from those individuals which did not molt or die within one week of respiration and excretion measurements (n = 28).

In all cases, data are expressed as a mean ± one standard error of the mean.

Results

Experiments A

Two series of experiments were conducted to determine the effects of a long (35 day) period of starvation on oxygen consumption and ammonia excretion by individuals of *G. ingens,* and to determine the influence of feeding history on these effects. In the first experiment, oxygen consumption and ammonia excretion rates of the five 1×/mo animals were determined prior to feeding. The animals were then fed on shrimp (n = 3) or salmon (n = 2). Respiration and excretion rates were determined again 12 hours after the food was removed (Day 1), and periodically throughout the 35 days of starvation. After 35 days, the animals were fed shrimp, and respiration and excretion rates were determined 12 hours (Day 1) and 60 hours (Day 3) after the food had been removed. In the second series of experiments, food was withheld for 35 days from animals previously fed 6×/mo (1st series). Respiration and excretion rates were determined periodically. After 35 days the animals were fed shrimp. Respiration and excretion rates were determined a final time 12 hours after removing the food.

Results of Experiments A

For the reasons stated in "Materials and Methods—Analysis of results", we have compared and contrasted the trends in rates in respiration and excretion, rather than the rates themselves.

The mean oxygen consumption rate of animals previously fed 1×/mo did not change significantly during 35 days of starvation (Fig. 1): the highest (Day 35) and lowest (Day 14) mean respiration rates are not significantly different ($P > 0.90$, paired t-test).

The mean ammonia excretion rate of these animals increased after the initial feeding and returned within 5–9 days to the prefeeding level of 0.253 ± 0.043 micromoles NH_3/g wet weight/h. By the fourteenth day the mean excretion rate had stabilized at a lower rate (0.114 ± 0.021 micromoles NH_3/g wet weight/h) and remained stable through the 35th day of starvation. Subsequent feeding again produced a large increase in mean ammonia excretion rate. The geometric mean atomic O:N ratio decreased on Day 1 as a result of the large increase in ammonia excretion, then increased gradually through the third week. Feeding again produced a sharp decrease in the O:N value.

The mean oxygen consumption rate of animals previously fed 6×/mo was stable through the twenty-first day of starvation, then decreased through the 35th day (Fig. 1). The final mean rate of 1.28 ± 0.20 micromoles O_2/g wet weight/h was 64% of, and significantly lower than, the initial post-digestive (Day 3) rate of 1.87 ± 0.17 micromoles O_2/g wet weight/h ($P < 0.05$, paired t-test). Subsequent feeding increased the mean oxygen consumption rate measured on Day 1 to 1.51 ± 0.18 micromoles O_2/g wet weight/h.

Ammonia excretion rates (Fig. 1) dropped rapidly in the first 5 days after feeding. The mean rate dropped again between the third and fourth weeks, and did not change significantly in the fifth week. Subsequent feeding produced a large increase

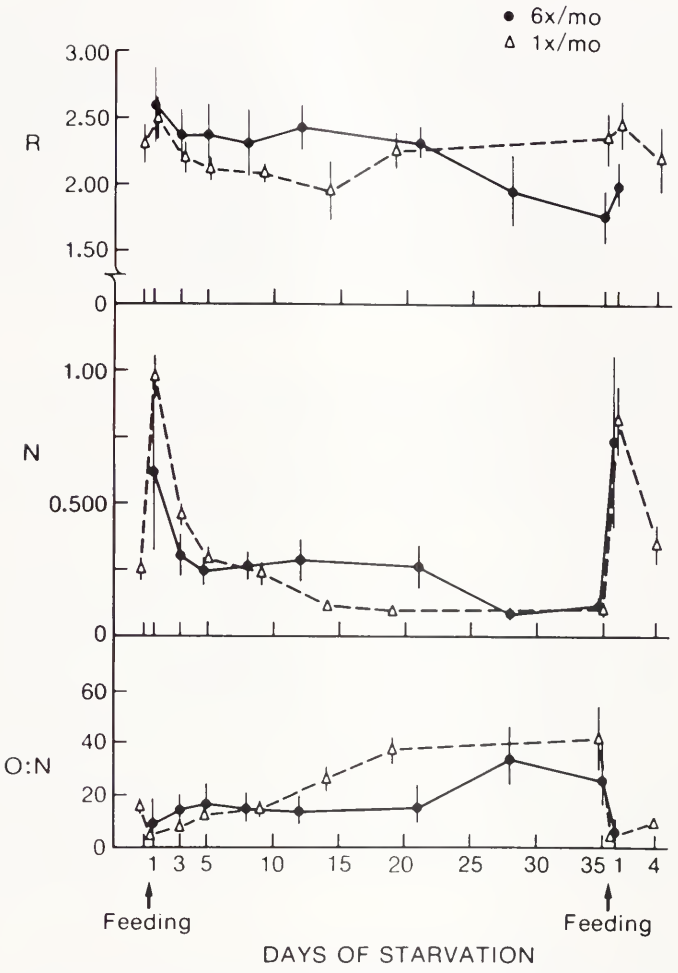

FIGURE 1. Oxygen consumption rates (R), ammonia excretion rates (N) and atomic O:N ratios of individuals previously fed either 6×/mo (n = 4) or 1×/mo (n = 5), during five weeks of starvation. Oxygen consumption and ammonia excretion rates are expressed in μmoles/g wet weight h^{-1}. Mean ± standard error.

in mean ammonia excretion rate on Day 1. The geometric mean atomic O:N ratio was stable at values of 24–26 from Day 3 through the third week of starvation and increased significantly in the fourth and fifth weeks ($P < 0.002$ for both weeks, when compared with Day 21, paired t-test).

The early response to starvation therefore differed between the two groups. The respiration and excretion rates of animals previously fed 6×/mo were higher in the first three weeks of starvation relative to rates after 35 days of starvation. The respiration rates of animals previously fed 1×/mo were more stable, and ammonia excretion rates stabilized within 2 weeks. The slower stabilization of the excretion rates of the 1×/mo animals, which caused a gradual increase in the O:N ratio, is probably due to the fact that, on the average, 1×/mo animals ate 2.5 times more per gram of animal weight at the initial meal than did animals fed 6×/mo.

Experiments B

Two series of experiments were conducted to determine the effects of feeding, feeding history, and food deprivation over shorter periods of time, on respiration and excretion rates. Respiration and excretion rates of animals previously fed 6×/mo (2nd series) or 2×/mo were measured periodically during two sequential periods of food deprivation, the first lasting 12 days and the second for 10 days. The experiments in each period began with individual measurements of rates made a few days before feeding. At the end of the 10 day fast, the animals were fed again and respiration and excretion rates determined 12 hours (Day 1) and 60 hours (Day 3) after food removal.

Results of Experiments B

The mean oxygen consumption rates of the two 2×/mo individuals were higher than those of the 6×/mo individuals in the first 12 day period (Fig. 2). The two groups did not otherwise differ in their responses to feeding or to this period of starvation, although a larger sample size is needed before conclusions can be drawn concerning differences between effects of these feeding frequencies on responses to short-term starvation.

The data indicate, however, that feeding induces transient increases in respiration and excretion rates in individuals of both groups. Mean oxygen consumption rates and ammonia excretion rates increased immediately after each feeding, then decreased to or below prefeeding levels sometime between Day 1 and Day 3 to Day 7. Feeding restored respiration and excretion rates to pre-starvation levels. However, the feeding "peaks" only briefly interrupted the continuing decreases in ammonia excretion rates in both groups. Consequently, the O:N ratios for individuals in both groups generally decreased on Day 1, indicating protein metabolism, and increased between feedings, indicating increasing reliance on non-nitrogenous energy sources. The more rapid increase in O:N ratios during the second period of starvation suggests that the metabolic shift to non-nitrogenous compounds occurred more quickly.

Meal size and animal weight

The amount of shrimp eaten at each feeding increased with increasing animal weight (Fig. 3). Meals eaten by an individual within a week before molting or dying and the first meal eaten after molting are omitted since the former are often small due to softening of the exoskeleton, and the latter are sometimes atypically large, probably due to the two week fast imposed after molting. The regression includes only data on the average meal sizes of animals which had been fed at least two quantified shrimp meals and were not affected by molting or death. There was no significant difference between the regressions for the three feeding regimes ($P > 0.75$, F-test). The overall regression of average meal size on animal wet weight is $M = 33.59 + 11.32W$ ($r = 0.70$, $n = 14$), where M = average mg AFDW eaten/meal, and W = wet weight of *G. ingens*, in grams.

Feeding "peaks"

We determined the correlation between increases in ammonia excretion rates and oxygen consumption rates which often followed feeding, and between the increases in each rate and the amount of food eaten, using the 28 data sets which satisfied the following criteria: (1) oxygen consumption and ammonia excretion rates

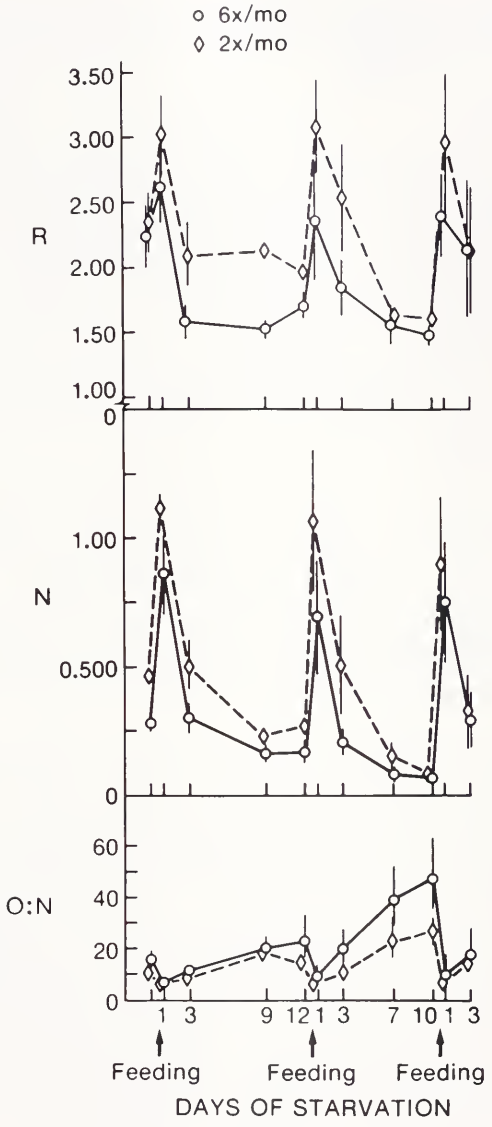

FIGURE 2. Oxygen consumption rates (R), ammonia excretion rates (N) and atomic O:N ratios of individuals which were alternately fed and starved. Individuals had previously been fed 6×/mo (n = 4) or 2×/mo (n = 2). Oxygen consumption and ammonia excretion rates are expressed in μm/g wet weight h^{-1}. Mean ± standard error.

were determined within two days before the animal fed (prefeeding rates), and again on Day 1 (12 hours) and Day 3 or 4 (60 and 84 hours, respectively) after feeding ceased (postfeeding rates); (2) the individual fed on shrimp, and (3) did not molt or die within one week after the meal. A "peak" was considered to have occurred in respiration or excretion if the rate measured on Day 1 was greater than both the prefeeding and postfeeding rates. The magnitude of the peak was calculated as the difference between the rate measured on Day 1 and the average of the pre- and post-

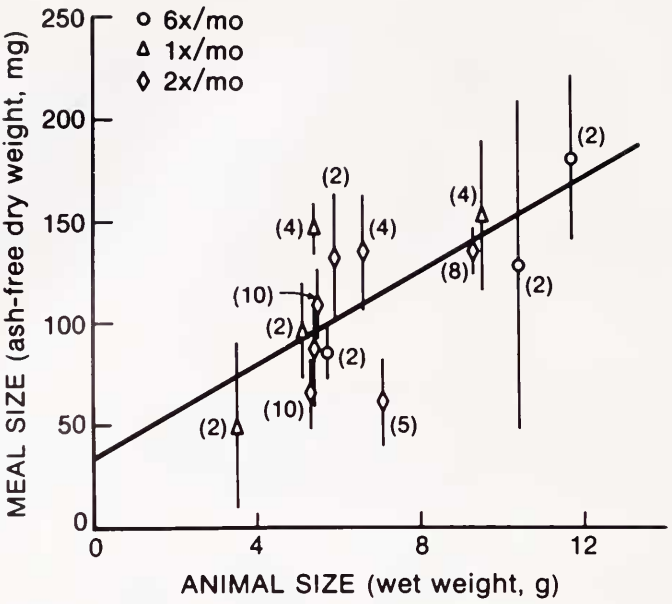

FIGURE 3. Meal size as a function of animal weight. Individuals were fed 1×/mo, 2×/mo or 6×/mo. Numbers in parentheses indicate number of shrimp meals contributing to the data point (mean ± standard error). Meals eaten by an individual within a week before molting or dying, and the first meal eaten after molting, are omitted. y = 33.59 + 11.32× (r = 0.70).

feeding rates. Peaks in ammonia excretion occurred in all 28 data sets, which involved 12 animals in the 6×/mo (2nd series), 1×/mo and 2×/mo groups. Peaks occurred in oxygen consumption in 71% of the sets (20 of 28).

The linear regressions of increase in ammonia excretion rate (E, in micromoles NH_3/h) on amount eaten (F, in mg AFDW) did not differ between the three regimes (Fig. 4; $P > 0.25$, F-test). The regression is E = 0.038F if it is constrained to pass through the origin, *i.e.,* if one assumes that the peaks in excretion are due to feeding. This regression does not differ significantly from the unconstrained regression ($P > 0.10$, F-test). Since 75% of the ash-free dry weight of the shrimp fed to *G. ingens* is protein (Childress, unpublished data), the regression of the increase in ammonia excretion (12 hours after feeding) on protein ingested (P, in mg) is E = 0.051P. The correlation between animal wet weight (y, in grams) and the magnitude of the postfeeding ammonia peak (x, in micromoles NH_3/h) is y = −4.98 + 10.44× ($P < 0.001$, *t*-test for significant slope). This is consistent with the positive correlation between meal size and the weight of *G. ingens.*

Although there was no significant linear correlation between the magnitudes of post-feeding oxygen peaks and the amount of food eaten ($P > 0.10$, t-test for significant slope), the probability of a peak in oxygen consumption occurring after feeding was much higher than the probability of a peak occurring in a set of three sequential measurements not separated by a meal ($P < 0.005$, ×2 test on a 2 × 2 contingency table). It is likely that measurements made over a longer period of time, or at a different point in the time course of the change in respiration rate, would have revealed a correlation between the magnitude of the peak in respiration rate and the amount of food eaten, since there is a significant positive correlation between the increases in rates of respiration and ammonia excretion (Fig. 5). The least-

squares linear regression of the increase in oxygen consumption (R, in micromoles O_2/h) on the increase in ammonia excretion (E, in micromoles NH_3/h) is R = 1.396 + 1.027E (r = 0.74, n = 20).

Discussion

The data obtained for individuals starved for 35 days indicate that the respiration rates of previously well-fed individuals are stable for several weeks of food deprivation before beginning to decrease. This suggests that activity levels of animals which have fed frequently prior to food deprivation may also be maintained during this period. A similar transient "plateau" in respiration rate, followed by a rate decrease, has previously been observed for two benthic, shallow water crustacean species during starvation (Wallace, 1973; Regnault, 1981). The stable mean respiration rate of the 1×/mo animals suggests that the respiration rates of the 6×/mo individuals would have stabilized at a lower level.

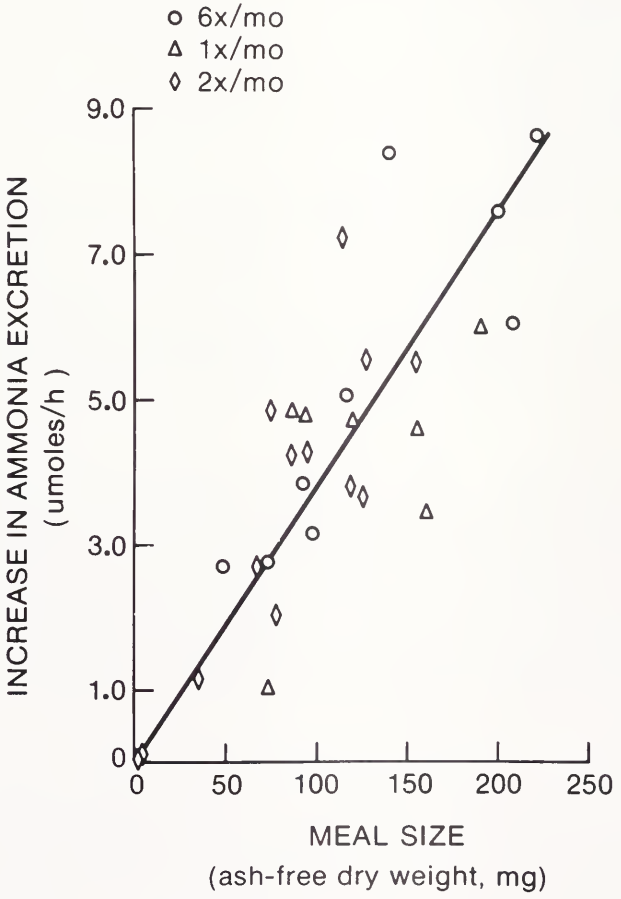

Figure 4. Postfeeding increase in ammonia excretion rate as a function of meal size. Shrimp were used for all meals. The increase in excretion rate is the difference between the rate measured 12 hours after feeding and the average of the rates measured before and 3–4 days after feeding. The regression is constrained to pass through the origin. y = 0.038×.

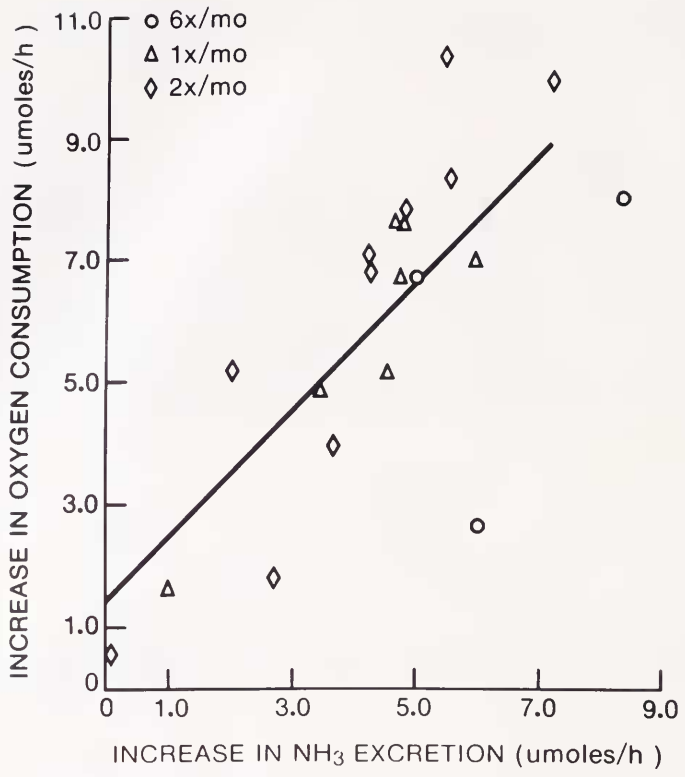

FIGURE 5. Postfeeding increase in oxygen consumption rate as a function of the postfeeding increase in ammonia excretion rate. The increase in each rate is the difference between the rate measured 12 hours after feeding and the average of the rates measured before and 3–4 days after feeding. $y = 1.40 + 1.03\times$ ($r = 0.74$).

The mean O:N ratios of the 6×/mo (1st series) individuals suggest that, when first deprived of food, previously well-fed individuals of *G. ingens* metabolize a large proportion of protein or other nitrogen-containing compounds relative to lipids and carbohydrates. The increase in the mean O:N ratios of starved individuals, which was also observed by Quetin *et al.* (1980), indicates that more lipid and/or carbohydrate is oxidized by the animals as the length of time without food increases. Lipids are probably a more important energy source for *G. ingens* during starvation than are carbohydrates since lipid typically comprises about 45%, and carbohydrate only about 0.6%, of the ash-free dry weight of an individual (Childress and Nygaard, 1974).

The responses of *G. ingens* to starvation are not unusual. Rates of respiration (Wallace, 1973; Mayzaud, 1976; Regnault, 1981) and ammonia excretion (Mayzaud, 1976) of a number of shallow water benthic and epipelagic crustacean species also decrease during starvation. This is not surprising since reduced energy expenditures are potentially advantageous during a prolonged period without food. Many invertebrate species appear to rely primarily on large lipid and/or carbohydrate reserves during starvation (Conover, 1964; Chaisemartin, 1971), while some species metabolize protein concurrently with lipid, as *G. ingens* appears to do (Schafer, 1968; Chaisemartin, 1971; Ikeda, 1971). A few species soon rely primarily on protein

metabolism when their smaller lipid and carbohydrate reserves have been exhausted (Cowey and Corner, 1963; Regnault, 1981).

Two factors suggest that *G. ingens* is better able to survive prolonged periods without food than are many shallow water species. The metabolic rates even of freshly-captured individuals of *G. ingens* and of other midwater animals are lower than those of shallower-dwelling marine animals (Childress 1971a, 1975), and the lipid content of *G. ingens* and of many midwater crustaceans is higher than that of many species living in shallower water (Childress and Nygaard, 1974). Considered together, the high lipid content, low metabolic rate, and similarity in response of individuals of *G. ingens* to starvation regardless of feeding history suggest that *G. ingens* and perhaps other midwater crustaceans are able to survive relatively long periods of food deprivation. This capability may be essential in a food-poor or patchy environment.

The similarities in the responses to starvation by all four groups of individuals suggest that the responses of field individuals to artificially imposed starvation will be similar in all seasons, and that the responses of individuals fed and starved in the laboratory are similar to the responses of field individuals confronted with natural variations in food availability.

The elevation in respiration rate after an animal has ceased feeding has been referred to as the "specific dynamic action," "calorigenic effect," and "heat increment" of food. Although protein ingestion appears to produce a greater increase in respiration rate than does ingestion of lipid or carbohydrate, the effect of each varies with the total composition of the food (Forbes and Swift, 1944). The importance of postfeeding increases in oxygen consumption to a valid estimation of a species' energy budget depends on the magnitude of the increases, which, for *G. ingens*, depends on meal size and feeding frequency. An estimate of the potential energetic importance of these peaks to *G. ingens* may be obtained by combining data on the probable average daily caloric intake by an individual with data on the caloric content of the ridgeback shrimp on which *G. ingens* was fed (0.515 cal/mg AFDW: Childress, unpublished data). Hiller-Adams (1982) has estimated that a 2.8 g instar 7 individual of *G. ingens* requires about 32 calories/day for growth and metabolism. This is equivalent to 156 mg AFDW of ridgeback shrimp every 60 hours. [The data on which the caloric requirement is based were obtained using individuals in instar 7; 2.8 grams is the mean weight of individuals in this instar (Childress and Price, 1978).] This would produce an ammonia peak of 5.9 micromoles/h (Fig. 4) and an increase in respiration of 7.5 micromoles 02/h (Fig. 5). Since the height of the postfeeding peak was calculated as the difference between the 12-hour postfeeding rate and the average of the prefeeding and 60-hour (or 84-hour) postfeeding rates, we assume that the additional oxygen respired may be approximated by the area of the triangle bounded by the peak and the average of the prefeeding and postfeeding rates. The "base" of the triangle is then 60 hours long, and the area is (30 hours) $\times$ (peak height, in micromoles O_2/h), or in this case, 225.3 micromoles O_2. If one assumes that a mmole of oxygen consumed represents an energy expenditure of 103.7 calories (Brett and Groves, 1979), 23.4 calories are expended in the postfeeding increase in respiration. This represents 29% of the calories ingested, and an 85% increase in the estimated average respiration rate of 4.4 micromoles O_2/h for an animal of this size. (The average respiration rate is calculated from the emperical relationship between size and respiration rate in Childress, 1971b). Since the protein content of fish and crustaceans which live in shallower water (and the shrimp on which *G. ingens* were fed in the laboratory) tends to be higher than that of pelagic midwater species (Childress and Nygaard, 1937, 1974), and since protein may cause

a relatively large portion of the postfeeding increases, we expect that the increases which occur in nature are somewhat smaller than those we have measured in the laboratory.

The percent increase in respiration which we have observed appears to be considerably larger than the 17–37% increase reported for juvenile lobsters (Capuzzo and Lancaster, 1979), and the 7–40% increase reported for juvenile *Macrobrachium rosenbergii* (Nelson *et al.*, 1977). The two species were fed several diets which differed in composition. These are the only other crustaceans of which we are aware for which quantitative data have been published. However, we determined the duration of the postfeeding increases. This was not determined in the previous two studies (postfeeding measurements were made within 24 hours of feeding), and might well affect estimates of the energetic importance of the postfeeding increases. Additionally, the percent increase for *G. ingens* is calculated relative to a postdigestive metabolic rate which is quite low relative to that of other crustaceans (Childress, 1971a). Among fish, "specific dynamic activity" accounted for 4–45% of the energy ingested by young coho salmon (Averett, quoted by Warren, 1971), $14 \pm 4\%$ (mean $\pm$ standard deviation) for largemouth bass (Beamish, 1974), and 5–24% for bluegill sunfish (Pierce and Wissing, 1974).

Data regarding the magnitude of the postfeeding increase in oxygen consumption by animals have often been expressed as a percent of the postdigestive metabolic rate in determining correlations with other parameters. However, since the increase in respiration is due to the food eaten by the animal it is not dependent on, and so should not be expressed (as many workers have) as a function of an animal's postdigestive metabolic rate in determining correlations. In addition, the data are more useful expressed as increases in the absolute amount of oxygen consumed, as we have done, rather than as a percent of postdigestive metabolic rate since the usual size-dependency of metabolic rates (larger animals tend to respire at a lower weight-specific rate) prevents the extrapolation of percent data to animals and meals of other sizes.

It should also be noted that our data indicate that metabolic measurements made within a day or two after feeding may not represent postdigestive rates, as has often been assumed for other species. Up to a week may be required before *G. ingens* achieves predigestive rates after having fed. Other investigators, working with teleosts (Beamish, 1974, Pierce and Wissing, 1974) have also found that several days may be required before animals are postdigestive.

The transient increase in ammonia excretion rates of recently fed individuals suggests that a significant portion of the amino acids in protein assimilated by *G. ingens* is rapidly deaminated. If one assumes that (1)75% of the AFDW of the shrimp food is protein (Childress and Price, unpublished data), (2) the protein is 16% nitrogen by weight (Kleiber, 1961), and (3) the total quantity of ammonia excreted as a result of feeding is the area of the triangle bounded by the postfeeding peak and the average of the prefeeding and 60-hour postfeeding rates, then *G. ingens* deaminated about 11% of the shrimp protein ingested within 60 hours of feeding. The remainder of the ingested protein apparently is incorporated into the animal's body.

The pronounced increases in respiration and excretion by *G. ingens* after feeding indicate that average respiration and excretion rates of individuals in the midwater environment depend strongly on ingestion. Post-digestive respiration and excretion rates may considerably underestimate average field rates of a species when food intake in the ocean is high.

In summary, *G. ingens* appears to rely largely on protein or other nitrogen-containing compounds when first deprived of food. Lipid reserves become more important to previously well-fed individuals after about three weeks without food. Respiration and excretion rates begin to decrease at this time. The stability of the respiration rate of 1×/mo individuals suggests that respiration stabilizes at a lower level. Transient postfeeding increases in respiration and excretion indicate that measurements of respiration and excretion rates using postdigestive animals underestimate the average rates in nature by an amount directly proportional to food intake. The energy expended in increased respiration is not negligible: about 29% of the caloric value of the ingested laboratory ration may be expended in postfeeding increases in respiration by an instar 7 individual.

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